A novel digital telemetry system for tracking wild animals: a field test for studying mate choice in a lekking tropical bird

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Summary

1. Radiotelemetry provides a tool for monitoring animals that are difficult to observe directly. Recent technical advances have given rise to new systems that present expanded opportunities for field research. We report the results of the first field test of Encounternet, a new digital radiotelemetry system comprising portable receiver stations and digital tags designed for long-term studies of the social behaviour and ecology of free-living animals.

2. We present results from a series of field tests designed to evaluate the utility of Encounternet for monitoring animals in a neotropical forest, with an emphasis on evaluating mate sampling behaviour in female long-tailed manakins. In this tropical species, females visit leks where males perform elaborate dances on horizontal perches. Females are highly cryptic in both plumage and activities, and therefore, Encounternet might provide unique insights into female behaviour and ecology.

3. Our first two tests revealed that pulse strength and probability of detection decrease with the distance between tag and receiver and that tags placed on a fixed perch near a receiver showed different patterns of reception than more distant tags. Our third test revealed that antenna angle had only a small influence on pulse strength.

4. Blind analysis of simulated bird movements confirmed that the Encounternet system provides reliable information on animal activity. Data from multiple receivers permitted accurate reconstruction of simulated bird movements. Tag detections showed low levels of false negatives and false positives.

5. Female manakins responded well to carrying Encounternet tags attached by an elastic leg harness. Birds flew well upon release and were detected for 7.5 ± 0.8 days after release. Recaptures and re-sightings of females were rare in our large study population, yet there were two occasions where we confirmed that the tag fell off within 1 year.

6. We conclude that Encounternet technology provides an effective tool for monitoring animal ecology and behaviour. We show that it is capable of providing accurate measures of distance and that it is a highly versatile system for studying the ecology and behaviour of free-living animals. We discuss the unique opportunities facilitated by this technology for future ecological and behavioural studies.

Key-words: animal tracking, digital telemetry, field research, mating activities, radiotelemetry

Introduction

Tracking technologies have revolutionized ecological research by allowing long-term monitoring of animal movement and behaviour. The ecological and behavioural insights provided by radiotelemetry (e.g. Hinch & Rand 1998; Westcott & Graham 2000), satellite transmitters (e.g. Weimerskirch *et al.* 2000; Hooker & Baird 2001), geolocators (e.g. Stutchbury *et al.* 2009; Montevecchi *et al.* 2012), microphone arrays (e.g. Blumstein *et al.* 2011), and related technologies have expanded

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our understanding of vertebrate biology beyond what was possible through direct observation or mark-recapture methods. Radiotelemetry, the most longstanding of these technologies, has facilitated monitoring silent or covert animal movements and behaviours and has become a widely used approach for monitoring animals (reviewed in Cooke *et al.* 2004; Ropert-Coudert & Wilson 2005). Movements of animals that cannot be studied through direct observation can be quantified effectively with telemetry.

Recent technological developments have produced new innovations in radiotelemetry, particularly because of the exponential enhancement in chip performance delivered by the semiconductor industry. Traditional radio receivers were handheld devices, and animals were monitored primarily while researchers followed the tagged animal with an antenna (Amlaner & MacDonald 1980). More recently, autonomous receivers allow animals to be monitored while researchers are absent from the area (Cooke *et al.* 2004). Consequently, animals can be monitored around the clock and without the influence of the presence of the researcher. Analogue transmitters broadcasting signals at different frequencies can be manually monitored by receivers that scan multiple channels (e.g. Crofoot *et al.* 2010). Recent developments in digital transmitters allow for multiple tags to transmit at the same frequency with unique codes. These technical advances dramatically increase the opportunities for radiotelemetry technology to be used in the study of the ecology and behaviour of wild, free-living animals. Until very recently, these advancements in digital radiotelemetry have only been available for large-bodied animals (e.g. Hazen *et al.* 2009).

Encounternet is a new radiotelemetry technology that brings the advantages of digital radio and automated monitoring to small animals for the first time. In an Encounternet system, tags as lightweight as 0·8 g are worn by small animals such as passerine birds (Fig. 1a,b). The tags are similar in form to an analogue radiotag, but rather than a fixed-function analogue radio circuit, these tags contain a programmable microprocessor and a digital transceiver, allowing much greater flexibility in tag functionality. Encounternet tags are equipped with digital interface ports and analogue data converter inputs, allowing tags to include sensors to log temperature, sound, acceleration, GPS location, etc. The tags can be configured via radio commands, and tags can operate in many modes, such as a conventional transmitter tag, a tag-to-tag proximity logger, a radio transponder or a radio repeater. The research described here – representing the first field test of this system – focuses exclusively on using Encounternet as a digital automated telemetry logging system, where each tag periodically broadcasts a brief digital radio pulse encoded with a unique ID number.

The second component of Encounternet is the wireless receiver station (Fig. 1c). Receiver stations contain a microprocessor, transceiver radio and a high capacity flash memory card. They function as automated monitoring devices, logging the ID number, time and signal strength of every tag pulse they receive. Receiver stations are environmentally hardened and powered by an external battery pack; with two rechargeable D-cell batteries, they can log radiotag pulses for weeks without maintenance. Receiver stations can be placed in strategic locations to monitor the presence and absence of tagged animals or be placed throughout the habitat to record the overall movement patterns of animals.

The third component of Encounternet is a manually operated 'master node' that serves as the user interface to the Encounternet tags and receiver stations. The master node consists of a modified receiver station mounted on a high-gain directional antenna and attached to a laptop computer running custom interface software. The master node is used primarily to wirelessly configure tags and receiver stations and to download tag ID pulse logs from receiver stations in the field. The master node can also operate as a radiotracking system to locate and track tagged animals, as in conventional radiotracking.
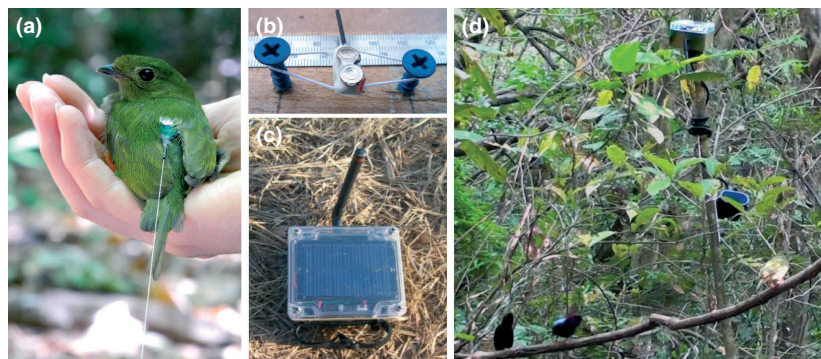

Fig. 1. Photographs of the components of the Encounternet automated telemetry system used in a field test to study long-tailed manakins in Costa Rica. (a) A female long-tailed manakin fitted with an Encounternet tag; the tag sits above her preen gland and the antenna runs down and beyond her tail. (b) An Encounternet tag, comprising two air-zinc batteries, an antenna and a programmable chip that controls the timing of the radio pulses. The components are embedded in epoxy for waterproofing, and an elastic thread is fed through Teflon tubes at the two ends of the tag to create a leg harness. Here, the tag is suspended between two blue screws. (c) An Encounternet receiver station; the receiver hardware is contained in a waterproof box, a cable that attaches to an external battery back, and a movable antenna is located on one side. (d) A screen capture from a video at a long-tailed manakin display perch. Two black males (lower left) dance on a display perch for a green female (lower right). The Encounternet receiver station (top) is mounted above the display perch and the external battery pack can be seen below it.

We tested the capabilities of Encounternet in a field test designed to evaluate the utility of this technology for studying the movements of small birds in a neotropical forest habitat. In particular, we were interested in using Encounternet to study female mate choice behaviour in long-tailed manakins (*Chiroxiphia linearis*), a neotropical suboscine passerine bird. In this lek-mating species, males congregate in small groups (3–13 males) where social relationships follow linear, age-graded dominance hierarchies (Foster 1977; McDonald 1989a,b). The top two males in the hierarchy, the alpha and beta, attract females to their display areas through vocal duets and then perform complex, cooperative dances for prospecting females on 'display perches', low horizontal branches in the forest understory (Fig. 1d; Foster 1977; McDonald 1989a,b). The display areas of long-tailed manakins can be characterized as exploded leks, where different leks are in visual but not acoustic isolation (Gilliard 1963; Foster 1977). Unlike most lek-mating species, however, females choose among alpha males at different leks rather than within males at a particular lek (McDonald 1989a). Mating success is highly skewed, with a small proportion of alpha males securing most of the copulations (McDonald 1989b; McDonald & Potts 1994). Previous studies have shown that synchronization of duets, duetting rates and components of male behavioural displays influence female mate choice decisions (McDonald 1989b; Trainer & McDonald 1995). Yet, we know little about how females go about selecting mates. Females rarely vocalize, they are very cryptic in both behaviour and appearance, and re-sighting data indicate that they have much larger home ranges than males (McDonald 1989b). If Encounternet provides reliable data, devices attached to female long-tailed manakins would facilitate tracking of female lek visitation behaviour and provide novel insight into female mate choice and male mate attraction behaviour.

In this study, we conduct the first field test of Encounternet telemetry technology. Our field test is designed to evaluate the efficacy of this system for research on the mating behaviour of female long-tailed manakins living in a dense neotropical dry forest. However, this versatile system is expected to be useful for tracking many species of animals in a wide variety of habitats and could be used equally well to study nest visitation, foraging behaviour, territory use and extra-pair forays, and social behaviour. We present a series of tests involving active Encounternet tags and receiver stations, each an investigation of the system's capabilities for studying the ecology and behaviour of females (Encounternet tags) as they visit male display perches (Encounternet receiver stations) in a natural environment.

1 We placed Encounternet tags at varying pre-determined distances from receiver stations and evaluated the signal strength values and the probability of detection of the tags across a range of distances; our goal was to quantify how detection varies when tagged animals change their distance from a receiver station.

2 We placed Encounternet tags on the display perches at long-tailed manakin leks and quantified variation in signal strength values and the probability of detection over time; our goal was to understand how detection varies when a tagged animal sits in a fixed position near a receiver station for a period of time.

3 We changed the angle of the Encounternet tag antennas relative to the receiver station antennas and evaluated whether their relative angles influence signal strength value or the probability of detection; our goal was to understand how detection varies as tagged animals change their orientation, but not distance, relative to receiver stations.

4 We conducted simulated 'flight tests' by moving active Encounternet tags around the forest to mimic the behaviour of female long-tailed manakins, and assessed how accurately the technology allows us to reconstruct the behaviour of the simulated females; our goal was to evaluate whether we could correctly record the movements of simulated female manakins in a blind test.

5 Finally, we evaluated how tagged female long-tailed manakins responded to being outfitted with an Encounternet tag and tested whether the receiver stations detected the tagged females after release.

We discuss the utility and versatility of this system for conducting future studies of female long-tailed manakins, for studying mate choice in lekking animals and for studying the ecology and behaviour of wild animals generally.

Materials and methods

GENERAL FIELD METHODS

Our field test of Encounternet took place in Sector Santa Rosa of the Guanacaste Conservation Area in northwestern Costa Rica from April to May of 2010 and 2011. This site is designated a World Heritage Site by the United Nations Educational, Scientific and Cultural Organization (UNESCO) and is home to the largest remaining stand of dry forest habitat in the neotropics. The study took place in the mature humid forest sections of this study site, where the thick vegetation makes direct observation of animals difficult (Mennill & Vehrencamp 2008). Moreover, wet tropical habitats are expected to limit the accuracy of telemetry (Millspaugh & Marzluff 2001) as well as the function of electronic equipment. Consequently, this habitat provides a challenging environment for testing the utility of a radiotelemetry system. Given that there was rarely line-of-sight contact between tag and receiver (except in test 3, see below), our field study provides a compelling test of the system's capacity to work amidst dense vegetation.

EQUIPMENT

The tags used in this field test were designed and built by the University of Washington Encounternet project (http://encounternet.net) and consisted of a 7×15 mm circuit board (Encounternet tag version 3a) containing a Texas Instruments MSP430 microprocessor and Texas Instruments CC1101 digital radio transceiver operating at 433 MHz, with a 16·5-cm steel-wire antenna attached (Texas Instruments, Dallas, TX, USA). Two size five zinc-air hearing aid batteries powered the tags. All components were embedded in an epoxy resin matrix for weatherproofing. Prior to placing tags on females, we used a green marker to colour the dried epoxy, so that the tag would blend in with the female's green plumage. Tags were programmed to trans-

mit a unique ID pulse every 4 s in 2010 and every 5 s in 2011 (we decreased the pulse rate to once every 5 s in 2011 to enhance tag battery life).

Receiver stations consisted of a circuit board (Encounternet receiver station version 1.1) with a Texas Instruments MSP430 microprocessor, Texas Instruments CC1101 digital radio transceiver operating at 433 MHz and a 2 GB Micro-SD flash card for data storage. Receiver stations were housed in a 9 × 9 × 6 cm waterproof ABS plastic enclosure and were powered by two rechargeable Imedion NiMH D-cell batteries in an external battery holder attached via a cable. A 12-cm omni-directional 433-MHz antenna was mounted on the case. Receiver stations were programmed to log all tag ID pulses to flash memory. Each log entry contained the ID of the receiver station and the tag, the time and date the ID pulse was received, and the received signal strength indication of the pulse.

We used an Encounternet master node for collecting data from the receiver stations in the field. The master node consisted of a modified receiver station attached to a directional Yagi antenna, with a serial cable connection to a laptop computer. To download logs from the receiver stations, we walked within *c.* 20 m of receiver stations and issued a command on the computer to initiate transfer of tag ID pulse logs from the receiver station to the memory card on the master node. Data downloaded from the receiver stations in the field were transferred to the computer and saved in a tab-delimited text file format.

Encounternet tags were attached to females with a figure-eight leg harness, modified from Rappole & Tipton (1991). Elastic thread was fed through two Teflon tubes embedded in the epoxy that coated the tag and tied off to create two loops that fit around birds' legs, so that the tag rode just above their preen gland, with the antenna running down and beyond the tail (Fig. 1). The elastic thread we used to create the leg harnesses consisted of a rubber inner core and an outer layer of braided cotton thread. So that the harness would deteriorate more quickly and fall off over time, we created a weak point in the outer layer, using a scalpel to cut the cotton threads in a small section of the harness near where the harness joined the tag, exposing the rubber inner core for a small section of the harness.

FIELD TESTS OF ENCOUNTERNET

To address the five goals of this study, we conducted a series of tests to evaluate the capabilities of Encounternet. The first three tests served to evaluate the system's capabilities in the field and calibrate the data collected by the receiver stations. The fourth test served to evaluate the accuracy of the system in measuring the behaviour of simulated female long-tailed manakins. The fourth test, based on the data collected in the first three tests, was a blind test (female movements were simulated by DJM; data were assessed by KAW, DFM and SMD). The fifth and final test was an evaluation of how female birds responded to the presence of the Encounternet tags.

For all of the tests below, the Encounternet receiver stations were mounted at fixed locations near male display perches at our field site. We mounted the receiver stations on a vertical branch as close as possible to the male display perch (0·3–1·4 m from the area where males would dance for females), at a height of *c.* 1·5 m (Fig. 1). We pointed the antennas for all receiver stations directly towards the ground.

TEST 1: VARIABLE TAG-TO-RECEIVER DISTANCES

Our first test involved recording the pulses from Encounternet tags at variable distances from the receiver stations. We attached tags to the top of a 1-m wooden pole and placed this pole at eight different distances from the receiver stations, measured with a measuring tape: 0·0 m (directly beneath the receiver station), 5·0, 10·0, 15·0, 20·0, 25·0 and 30·0 m. At each position, we rested the pole on the ground, so that tags were consistently 1 m above the ground, and we manually rotated the pole at a rate of *c.* six rotations per minute, to simulate the subtle movements of a bird making small perch changes while sitting on a branch, and to simultaneously rule out an effect of a particular angle of the tag antennas in this test. Tags were recorded at each position for 60 s. We conducted this test at *n* = 24 different sites (each with a different receiver station) using *n* = 8 different tags at each site. The study site is densely vegetated (Mennill & Vehrencamp 2008), and therefore, our tests demonstrate that the system is robust to dense vegetation.

TEST 2: VARIATION BETWEEN RECEIVER STATIONS

Our second test involved recording pulses from Encounternet tags that were set atop male display perches. We placed tags on the perch in an orientation that matched the way tags would sit when females visit the perch, with the antenna perpendicular to the axis of the perch and hanging down slightly below the horizontal. In the wild, female long-tailed manakins vary where they sit on the display perch during courtship visits, resulting in on-the-perch distances that may vary by *c.* 2 m relative to the receiver stations. During this test, we placed the tags near the centre of the perch at a distance of *c.* 0·3–1·4 m from the receiver station (see below), whenever possible in places where we had seen females sit at that particular perch. We held the tag still and recorded pulses for 60 s. We then rotated the tag by 180 degrees and recorded pulses for another 60 s with the tag at the opposite, perpendicular angle. We conducted this test at *n* = 64 different display perches (each with a different receiver station) using *n* = 5 different tags during each test.

TEST 3: VARIATION WITH ANTENNA ANGLE

Our third test was an assessment of whether the recorded pulses varied with the angle of the Encounternet tag antenna relative to the receiver station antenna. We mounted tags on a pole, as in test 1, and positioned the tags exactly 2 m from the tip of the downwards-oriented antenna of the receiver station. We held the orientation of the tags' antennas steady for 60 s, pointing the antennas towards the receiver station and parallel to the ground. We then rotated the tags by 90°, so that their antennas pointed at a direction orthogonal to the receiver antenna and parallel to the ground. We conducted this test at *n* = 9 different display perches (each with a different receiver station) using *n* = 2 different tags at each site. We did not test the effects of inverting the tags because long-tailed manakins do not usually orient themselves in this fashion (such an orientation might occur when studying a foliage gleaning species, for example). In theory, both dipole and monopole whip antennas emit a pulse in an even cylindrical pattern along their length, such that inverting a tag should have no effect on detectability. Yet future studies where such inversions are likely should quantify the effect it may have on detection. During each trial, we held the tags in a position with no vegetation in the space between the tags and receiver station.

TEST 4: SIMULATED FEMALE BEHAVIOUR

Our fourth test involved simulating female movement behaviour, to test the accuracy of the system for measuring the behaviour of female long-tailed manakins. In the field, we mounted two active Encounternet tags on the end of a 1-m wooden pole and carried the pole around

the forest, positioning the tags near the active receiver stations that were mounted at the display perches for all known leks in the study area. The field tests were conducted by DJM, and the data were analysed by KAAW, DFM and SMD, who were blind to all aspects of the path the tags had travelled in the field. We conducted 11 tests with 22 different tags, including two tags in each test to check that the system produced similar results for both tags. Each tag was carried to 2–5 receiver stations (average $\pm$ SE, 3·1 $\pm$ 0·3) and was set on the perch (thereby simulating a female sitting on the display perch), or at a 5 m horizontal distance from the perch (thereby simulating a female perching nearby, but not alighting on the display perch), and held at each position for 1·0–8·0 min (average $\pm$ SE, 2·68 $\pm$ 0·25 min).

After downloading the data from all receiver stations, we established a method for determining whether females visited the male display perch (as would a female inspecting males performing a courtship dance on the perch) or sat at a position $\geq$5 m away from the display perch (as would a female listening to the vocalizations of males or watching them from afar, but not directly inspecting a courtship dance). Based on the data from test 1, we calculated a signal strength threshold that would be consistent with a tag emitting pulses from the display perch or from $\geq$5·0 m away from the display perch. We calculated the threshold in three different ways based on how much data we had collected for each receiver station. (i) For perches where we had data from both test 1 and test 2 ($n = 24$), we calculated the threshold as the difference between the lower 25th percentile of the on-the-perch tag test data and the upper 25th percentile of the 5·0 m tag test data. (ii) For perches where we had data from test 2, but not test 1 ($n = 64$), we calculated a threshold as the lower 10 percentage of the on-the-perch tag test data (we determined this cut-off from the average percentage of on-the-perch tag test points that fell below the threshold of each perch from the previous method). (iii) For perches where we had data from neither test 1 or test 2 ($n = 24$), we calculated the population average values of the difference between the lower 25th percentile of the on-the-perch tag test data and the upper 25th percentile of the 5·0 m tag test data and used these values to determine our threshold. Based on the data from test 2 (see Results), it was clear that signal strength values at fixed distances fluctuate over time. We therefore used a criterion of three detections within a 30-s period at the appropriate thresholds to conclude that a female was present on or near the display perch. If fewer than three detections were recorded, we concluded that the tagged bird had moved through the area without stopping. The length of the visit was determined as the beginning of such a 30-s period, until the last tag detection that fell within the appropriate threshold. An example of one simulated female visit from this test is included as Data S1 in Supporting Information.

TEST 5: RESPONSES OF FEMALES TO WEARING ENCOUNTERNET TAGS

Our final field test involved evaluating the behaviour of female long-tailed manakins fitted with an Encounternet tag and determining whether tagged females were detected in the study site after release. Including the harness, tags weighed 0·88 $\pm$ 0·01 g ($n = 12$ measured tags) females weighed 18·76 $\pm$ 0·43 g (mean $\pm$ SE for the $n = 12$ females carrying these tags). Therefore, the tags weighed 4·69% of the female's body mass, less than the 5% body mass guideline that is thought to be appropriate for radiotagging wild birds (Caccamise & Hedin 1985; Naef-Daenzer 1994). This research follows established

guidelines for telemetry on wild birds, and was approved by the University of Windsor Animal Care Committee (permit AUPP #10-07).

STATISTICAL ANALYSIS

For tests 1 through 4, we evaluate two response variables. (i) *Signal strength* is a numerical estimate of how close the Encounternet tag is to the receiver. Signal strength values are whole numbers that vary on an arbitrary scale from −50 to 25 corresponding to a logarithmic representation of signal pulse amplitude (in dB), where lower, negative numbers imply large distances between tag and receiver, and higher, positive numbers imply small distances between tag and receiver. Each pulse received by an Encounternet receiver station records the date, time and identity of the signal, as well as the pulse's signal strength value. When tags were left at a particular distance or orientation for a period of time, we calculated an average signal strength value. (ii) *Probability of detection* is the proportion of total tag pulses received, where the numerator is the number of pulses recorded by the receiver station and the denominator is the number of pulses emitted by the tag.

We used linear mixed models to analyse signal strength and probability of detection, our response variables. To control for the fact that some tags were sampled repeatedly and that each receiver station was sampled at multiple distances (test 1), we included tag and receiver station identity as random factors. We used the expected means-squares approach for our linear mixed models, and we report *post hoc* Tukey's tests of honestly significant differences for significant main effects. Our sample sizes vary across the four tests because there were instances where pulses were not detected (for example, in cases where there was a substantial distance between the tag and the receiver station). All statistics were conducted in JMP 8.0 (SAS Institute, Cary, NC, USA). All tests are two-tailed, and all values are presented as means $\pm$ SE.

Results

TEST 1: VARIABLE TAG-TO-RECEIVER DISTANCES

The strength of Encounternet tag signals detected by receiver stations decreased significantly with the distance between tag and receiver (Fig. 2, linear mixed model; whole model: $F_{34,405} = 124\cdot6$, $P < 0\cdot0001$; fixed effect of distance: $F_{6,405} = 599\cdot3$, $P < 0\cdot0001$). For example, signal strength varied from 15·1 $\pm$ 0·5 for tags directly under the receiver station to −15·5 $\pm$ 1·3 for tags 30 m away. A *post hoc* test revealed significant differences between distances of 0, 5, 10 and 15 m between the tag and the receiver station, with overlapping signal strength values for 20, 25 and 30 m (Fig. 2). The random effects in the model revealed significant individual variation both for tags (random effect: $F_{7,405} = 4\cdot7$, $P < 0\cdot0001$) and receiver stations (random effect: $F_{21,405} = 21\cdot8$, $P < 0\cdot0001$).

The proportion of pulses detected by the receivers also decreased with the distance between the receiver and the tag (Fig. 2, linear mixed model; whole model: $F_{34,695} = 70\cdot2$, $P < 0\cdot0001$; fixed effect of distance: $F_{6,695} = 288\cdot2$ $P < 0\cdot0001$). For example, the proportion detected varied from 96·2 $\pm$ 2·6% for tags positioned directly beneath the receiver station to 4·4 $\pm$ 2·6% for tags positioned 30 m from
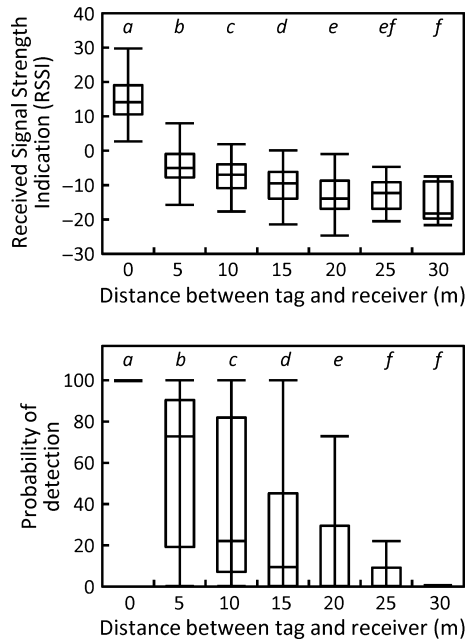
Fig. 2. The signal strength (top) and the probability of detection (bottom) decreased with the distance between Encounternet digital tags and receiver stations in a neotropical forest in Costa Rica. Box plots show the full range of data for the mean values from each receiver station; the boxes show the 25th, 50th and 75th percentile, and the whiskers show the maximum and minimum value. Letters above the box plots show the results of a *post hoc* test of honestly significant differences; plots that are not connected by the same letter are statistically different.

the receiver station. A *post hoc* test revealed significant differences in the proportion of pulses detected between all distances except for 25 m vs. 30 m, which were similarly low (Fig. 2). The random effects in this model also revealed significant individual variation for both tags (random effect: $F_{7,695} = 4.0$, $P = 0.003$) and receiver stations (random effect: $F_{21,695} = 27.8$, $P < 0.0001$).

TEST 2: VARIATION BETWEEN RECEIVER STATIONS

The global average signal strength value for Encounternet tags placed on male long-tailed manakin display perches was 5.1 ± 0.7. A test of tags set on display perches for 2 min revealed variation from one receiver station to the next (linear mixed model; whole model: $F_{34,693} = 70.2$, $P < 0.0001$; fixed effect of receiver station: $F_{41,695} = 122.2$ $P < 0.0001$; random effect of tag: $F_{4,695} = 208.0$, $P < 0.0001$). The average signal strength values varied between display perches from -14.4 to 25.0. This variation likely arose in part owing to variation in the distance between the display perch and the receiver station (range, 0·3–1·4 m), reflecting differences in the nearest vertical branch for mounting the receiver station.

One important goal for future studies of long-tailed manakin mating behaviour is distinguishing between females who travel near to a display perch (i.e. prospecting females assessing males from a short distance) and females who visit a display perch (i.e. prospecting females watching males dance at close
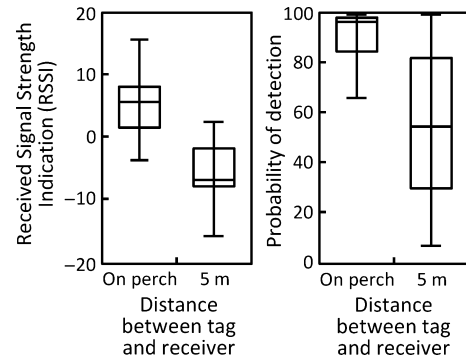

Fig. 3. The signal strength (left) and the probability of detection (right) were significantly higher for tags placed on the display perches of long-tailed manakins (approximate distance of 0·3–1·4 m) than for tags placed 5·0 m from the receiver station. Box plots show the full range of data for the mean values from each receiver station; the boxes show the 25th, 50th and 75th percentile, and the whiskers show the maximum and minimum value.

range). We found that Encounternet tags positioned on the display perch had significantly higher signal strength values than tags positioned 5 m from the receiver station (Fig. 3, paired *t*-test: $t_{23} = 5.7$, $P < 0.0001$, $n = 24$ receiver stations where we collected on-the-perch and 5 m-from-perch data using the same tags). Consequently, differences in signal strength can be used to distinguish females visiting male display perches from females observing display perches from a short distance. Tags positioned on the display perch recorded a statistically higher proportion of pulses, compared to tags positioned 5 m from the receiver station (Fig. 3, paired *t*-test: $t_{23} = 11.5$, $P < 0.0001$, $n = 24$ receiver stations).

TEST 3: SIGNAL STRENGTH AND TAG ANTENNA ANGLE

The signal strength of pulses from Encounternet tags held at a distance of 2 m with antennas oriented parallel to the receiver antennas (signal strength, 5.8 ± 3.5) was higher than when tag antennas were oriented perpendicular to the receiver antennas (signal strength, 3.1 ± 3.3; linear mixed model; whole model: $F_{10,25} = 1.6$, $P = 0.18$; fixed effect of orientation: $F_{1,25} = 5.8$ $P = 0.02$; neither random factor showed a significant effect: tag: $F_{1,25} = 0.33$, $P = 0.33$; receiver station: $F_{8,25} = 1.1$, $P = 0.39$). The difference between the means was subtle (parallel, 5·8; perpendicular, 3·1), and the ranges for parallel antennas (minimum, −4·1; median, 5·8; maximum, 10·4) and perpendicular antennas (minimum, −1·7; median, 2·9; maximum, 11·2) were overlapping. The probability of detection was 100% for both tag orientations at a close proximity to the receiver station (2 m with no intervening vegetation).

TEST 4: SIMULATED FEMALE BEHAVIOUR

Our blind analysis of simulated flights and perch visits of female long-tailed manakins showed that the Encounternet system can capably reconstruct the behaviour of moving animals. The tags were set on 28 display perches, simulating prospecting females arriving to inspect males during their dance

displays, for an average 'perch visit length' of 2·62 ± 0·30 min. Our blind analysis detected 27 of the 28 simulated perch visits (96·4%; i.e. a 'false-negative' rate of 3·6% for on-the-perch visits) and measured an average perch visit length of 2·53 ± 0·33 min. The Encounternet-estimated perch visit length showed a strong correlation with the actual perch visit length (Pearson correlation: $r = 0·87$, $P < 0·0001$, $n = 27$). The blind test of perch visits also detected four 'false positives' where Encounternet incorrectly indicated that a tag was placed on the display perch (i.e. a 'false-positive' rate of detection of 12·9% for on-the-perch visits). In all four cases, the system incorrectly identified a tag that was placed on a branch *c.* 5 m from the display perch as being positioned on the perch. The perch visit length for the false-positive visits (6·5 ± 1·4 tag pulse detections per visit, $n = 4$) was significantly shorter than the perch visit length for the true visits (29·0 ± 4·2 tag pulse detections, $n = 27$; unpaired *t*-test: $t_{29} = 2·0$, $P = 0·05$).

During the 'flight tests', the tags were also set on 26 branches that were *c.* 5 m from display perches, simulating females coming near to male display perches but not visiting the perches directly, for an average visit length of 2·95 ± 0·26 min. Our blind analysis detected 25 of the 26 simulated near-the-perch visits (96·1%; i.e. a 'false-negative' rate of detection of 3·9% for 5 m-from-the-perch visits) and measured an average perch visit length of 2·88 ± 0·39 min. The Encounternet-estimated perch visit length showed a positive correlation with actual perch visit length for tags placed *c.* 5 m from male display perches, although this relationship was not as strong as for tags placed on male display perches (Pearson correlation: $r = 0·48$, $P = 0·02$, $n = 25$). Our blind analysis detected an additional 27 instances of Encounternet detecting a female ≥5 m from the display perch; all 27 were cases where the researcher carrying the tag through the forest walked in the vicinity of the receiver (estimated closest distances of approach, 10–30 m), but did not pause to alight the tags on a branch. The perch visit length for these 27 visits (5·1 ± 2·9 tag pulse detections per visit, $n = 27$) was significantly shorter than the perch visit length for the true visits (23·7 ± 3·0 tag pulse detections per visit, $n = 26$; unpaired *t*-test: $t_{51} = 4·4$, $P < 0·0001$).

TEST 5: RESPONSES OF FEMALES TO WEARING ENCOUNTERNET TAGS

Females responded well to being fitted with tags. During a 2-year period, we tagged 82 females. In 79 cases, the female flew well on release, gaining altitude and perching in the mid-story at distances of 20–50 m and preening before flying out of sight, or flying out of sight immediately upon release. In the remaining three cases, females flew only a very short distance and landed on a low perch or on the ground. In the first case, the female made a second, normal flight soon thereafter and flew off without any further sign of impediment. In the second case, we attempted to minimize stress on the female by leaving the area while she was perched on a low branch; when we returned later, she had left the area. In the third case, when the female made a second strained flight, we immediately recap-tured the bird and removed the tag; she showed no further sign of impediment on re-release without the tag.

Seventy of the tagged females were detected moving around the area near the receiver stations for days to weeks after being tagged; the remaining females were not detected after the day they were released. Encounternet-tagged females moved around the study site, generating 46,222 detections by the receiver stations (Fig. 4). There were many detections with a signal strength value of 0–2 (Fig. 4a), which may be indicative of females sitting on male display perches. We calculated the length of female visits to male display perches and found that most visits were brief (3·8 ± 0·2 min; range, 12 s to 86 min; Fig. 4b).

The average length of time from tag deployment to final detection was 7·5 ± 0·8 days (range, 1–24; $n = 70$). We do not have sufficient data to determine whether the batteries in the tags died after this period or whether females exited the area (female home range can be as large as 80 ha; McDonald 1989b). In 2010, we located the active nests of two tagged females; in both cases, the female was engaging in normal nesting activities and did not show any sign of impediment because of the presence of the Encounternet tag.

Our study population is very large, and recapturing or re-sighting females is a rare occurrence, making it difficult to
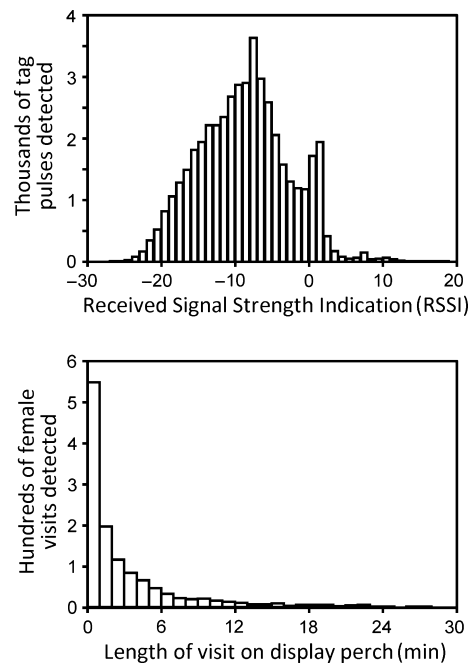

Fig. 4. Summary data from $n = 70$ female long-tailed manakins carrying Encounternet tags as detected by autonomous receiver stations at male display sites in a tropical forest in Costa Rica. A histogram of the strength of the received pulses (top) shows a high number of pulses with an received signal strength indication (RSSI) value of 0–2; these may be indicative of females observing male courtship displays while visiting a male display perch. A histogram of the length of female visits to male display perches (bottom) shows that most female visits to male display perches were brief, although hundreds of visits were longer. Twenty visits longer than 30 min are excluded from the histogram; the longest visit detected in this data set was 86 min.

confirm what proportion of the tags fell off over time. In 2011, we re-sighted three females who had been tagged previously (two were detected visually in the field; one was detected on a video recording of a display perch). Two females who were tagged in 2010 had lost their tags. One female who was tagged earlier in 2011 was still wearing a tag that was no longer transmitting (25 days between tagging and re-sighting).

Discussion

The results of our field test of an Encounternet telemetry system demonstrate that this new technology provides a compelling tool for automated tracking of animal movement in the challenging field environment of a tropical forest. The system, comprising digital radiotags worn by free-living animals and small receiver stations that autonomously log encounters with tags, met our expectations during a series of five tests. The tests were designed to evaluate the efficacy of the system for research on the mate choice behaviour of females (i.e. animals carrying Encounternet tags) relative to the display perches of tropical manakins (i.e. the Encounternet receiver stations). (i) Encounternet tags showed significantly higher signal strength values and probability of detection as the distance between tag and receiver decreased, demonstrating that Encounternet can quantify the distance between a tagged animal and a receiver station. (ii) Signal strength values were consistently higher when tags were placed on display perches compared to distances ≥5·0 m from display perches, demonstrating that Encounternet can distinguish between tagged animals near the receiver station vs. more distant animals. (iii) Tag vs. receiver antenna orientation influenced signal strength, but not probability of detection, yet this variation was small in comparison with variation owing to distance, demonstrating that tag orientation will have only a small influence when monitoring freely moving tagged animals whose antennas vary in orientation over time. (iv) Importantly, blind analysis of simulated long-tailed manakin movements demonstrated that the system can provide accurate reconstructions of the movement of Encounternet tags, with low rates of false-positive and false-negative detections. (v) Females responded well to being fitted with Encounternet tags, and anecdotal records demonstrate that tags fell off over time. The receiver stations produced more than 46,000 detections from 70 tagged animals and capably quantified the length of visits made by tagged animals to male display perches. Taken together, these results confirm that Encounternet provides an effective tool for measuring and monitoring the movements of tagged birds in a tropical forest. This is the first field test of this new technology.

Long-tailed manakins exhibit a unique and complex mating and social system (McDonald 2010), and Encounternet offers a special opportunity for understanding the behavioural ecology and evolution of this tropical bird. Males form social groups structured by linear dominance hierarchies, and entice prospecting females to mate by performing complex acoustic displays (Trainer & McDonald 1995), showcasing multiple elaborate plumage ornaments (Doucet *et al.* 2007), and performing intricately coordinated visual displays at their dis-

play perches (McDonald 1989b). Whereas males are conspicuous and reliably found in the same location, females are highly camouflaged (Doucet, Mennill, & Hill 2007) and their movement patterns are elusive. Consequently, the behavioural patterns of females are difficult to measure. In a study of this species at a different site in Costa Rica, McDonald (2010) collected an incredible data set on female visitation through thousands of hours of visual observations (15,000 lek observation hours over an 18-year period) at a relatively small number of lek sites (6–8 lek areas per year). Such intensive data collection is expensive and time-consuming. By contrast, automated detection by Encounternet permits vastly extended sampling opportunities. For example, in our 2-year study, we collected *c.* 40,000 lek observation hours at dozens of lek areas per year and were able to track individual females between each of the monitored leks. Therefore, Encounternet presents novel opportunities for understanding topics as varied as female mate sampling behaviour to the influence of male ornaments on female visitation.

One important concern for telemetry research is the influence of tag weight and the attachment mechanism on the animal's well-being (Naef-Daenzer 1994; Dixon 2011). One common guideline for birds is that the weight of all components attached to a bird should be < 5% of the bird's mass (Caccamise & Hedin 1985). Tracking studies of a variety of birds confirm that tags weighing < 5% of birds' body mass allow animals to continue normal activities, in species as varied as hooded warblers (*Wilsonia citrina*; Neudorf & Pitcher 1997), jackass penguins (*Spheniscus demersus*; Heath & Randall 1989) and Javan hawk-eagles (*Spizaetus bartelsi*; Gjershaug *et al.* 2004). Our analysis of 82 tagged tropical long-tailed manakins suggest that these birds can capably handle the presence of Encounternet tags weighing < 5% of their body mass. Of 82 tagged female long-tailed manakins, 79 flew well upon release, two struggled with their first flight but appeared to quickly recover and adapt to the tag's presence, whereas one bird was quickly recaptured, so that the tag could be removed. Our field experience suggested that minimal handling time and minimal banding stress produced the optimal results for females upon release. We therefore recommend that other researchers attach tags and release birds as quickly as possible, without additional stressors such as bleeding or intensive morphological measurements, to minimize stress.

Recapture and re-sighting of birds in our large study population is very rare, but multiple lines of evidence confirm that tagged birds continued to move through the study population. (i) Our receiver stations continued to encounter birds moving through the study site for extended periods after release (Fig. 4); their activities are the subject of forthcoming behavioural studies (K-A.A. Ward, D.F. Maynard, D.J. Mennill & S.M. Doucet, unpublished data). (ii) Two tagged females were found at their nest and were engaged in normal parental activities. (iii) Three tagged birds were re-sighted after extended periods in the wild; all three were engaged in normal activities, and two birds re-sighted a year after release had lost their tags.

Encounternet has many possible applications in future studies. Encounternet systems will be useful whenever tracking of

animals relative to fixed-position receiver stations provides information on the behaviour and ecology of tagged animals. In our study, we focused on female birds visiting lek sites; however, this system may be used to monitor a variety of animals and is applicable to a variety of mating systems. For example, Encounternet can monitor visitation to nests, food sources, water sources, roosting locations or sites where animals interact socially. By examining the timing of when multiple tagged animals are present at the same site, this system can be used to passively monitor social interactions over time. Encounternet can also be used to monitor habitat selection at different scales. Receivers can be set up at specific sites-of-interest, as we did in this study. Alternatively, receivers can be set up in a grid-like pattern throughout a study site to monitor spatial and temporal use of habitat; the size of the area monitored will be limited by the fact that receivers can detect tags at distances of up to 30 m. Such an application would provide a compelling approach to study species of conservation concern, to better understand movement and habitat use patterns (Rasmussen & Litzgus 2010). General coverage of a study site with receivers can also be used to identify territory boundaries and to monitor resident excursions into neighbouring territories (e.g. for covert animal movements, such as extra-pair copulations; Double & Cockburn 2000). Our field trials reveal ample variation in signal strength and detection probabilities between individual receiver stations (Fig. 2), demonstrating that future research should conduct similar tests and calibrate receivers to ensure accurate spatial monitoring.

As an autonomous detection tool, Encounternet has enhanced capabilities beyond previous technologies for automated monitoring of tagged animals. Radio frequency identification (RFID), usually involving passive integrated transponder devices (PIT tags), is a widely used technology also involving small devices worn by animals that are detected by fixed-position receivers (Bonter & Bridge 2011). PIT tags require no battery, and therefore, the devices are lightweight and provide information over extended periods (Gibbons & Andrews 2004). Although Encounternet tags are heavier and have finite battery life, they are capable of transmitting signals that can be detected at distances of at least 30 m (Fig. 2), whereas PIT tags can typically be detected at ranges of ≤0·1 m. An RFID system could not be used in the application we were testing here, for example, because the length of the male display perch (1–2 m) would require many PIT tag readers. The other established technology most similar to the one we tested here is the use of receiver towers in radiotelemetry studies, where multiple telemetry towers can triangulate the position of tagged animals (e.g. Kays *et al.* 2011; Taylor *et al.* 2011). This technology has similar limitations to Encounternet in terms of tag weight and tag battery life. Tower-based telemetry, however, is limited by the logistics and cost of setting up the large towers, the transmission of tag signals over long distances to be received by the towers and by the scale of resolution. Encounternet receiver stations are small and easy to set up (e.g. we easily set up 40 receiver stations in just a few hours) and facilitate positioning of birds on the scale of metres. It is worthwhile to note that tower-based telemetry is compatible with

Encounternet, and the two systems could work in concert. Encounternet is an affordable system comparatively, with a current approximate cost of $300 per receiver station and $250 per tag (USD).

In conclusion, our field test of Encounternet digital telemetry confirms that this system provides a compelling approach for monitoring wild birds. The results of trials designed to evaluate the efficacy of the system for monitoring long-tailed manakins can be readily applied to studies of other animals. A forthcoming iteration of this technology will permit tags to receive pulses from each other, and this development will facilitate unprecedented quantification of animal social interactions, extra-pair behaviour or other behaviours that are difficult to quantify. Uniquely, Encounternet provides round-the-clock monitoring of tagged animals and represents a significant advance in the study of animal ecology and behaviour.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Data S1. Spreadsheet showing example Encounternet data.

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